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ARE PLANTS OF SEA BEACHES AND DUNES TRUE HALOPHYTES?[1]

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IT seems to be generally implied, and in some cases expressly stated, by writers on ecological plant geography that the sands of the seashore, even at some distance above high tide, are impregnated with sodium chlorid and other readily soluble salts in quantity sufficient to determine the character of the vegetation. Thus, Contejean[2] gives the reader the impression that his second zone of strand vegetation in southwestern France, that of the beach proper, flourishes in a saline soil. Warming[3] writes: "The vegetation of the sand strand . . . . is a halophytic vegetation, because sand along the sea contains salt and the salty ground water comes close to the surface." Schimper,[4] describing the "Barringtonia formation" of trees and shrubs that occupies the higher beaches in tropical Asia and is separated from the high tide limit by a strip of bare sand devoid of vegetation, states: "It is the salt content of the soil which [here], as in the mangrove [formation] has called forth the most varied means of protection against transpiration. To the same factor is perhaps to be ascribed the rarity of thick [stemmed] lianas, growths which only flourish when the conditions for water-absorption are most favorable." Again, in his *Pflanzengeographie* (p. 688), he writes: "The cliffs [along the seashore] possess a less distinctly halophytic flora than the sandy and especially the marshy strand"—clearly implying his belief that the sand strand is a halophytic environment.

On the other hand, Massart,[5] who has investigated the vegetation of the Belgian strand, quotes an analysis of dune sand, giving only 0.02 parts of matter soluble in water in 100 parts of soil, and remarks: "It is therefore erroneously that the soil of the dunes is often considered as strongly impregnated with lime and with sodium chlorid. This opinion is justified only in the case of the seaward slope of the line [of dunes] nearest the beach and for the little valleys that penetrate it; hither the wind constantly carries the spray from the waves and fragments of shells, which it piles up on the strand. But as one goes farther from the sea, one encounters no longer anything but pure sand; what sea salt is carried so far is quickly washed out; the débris of shells is disintegrated and dissolved by carbon dioxid; and the calcium carbonate, in turn, is carried away by rainwater. Thanks to the sandy character of the soil, this filters rapidly downward."

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[1] Published by permission of the Secretary of Agriculture.

[2] Géographie Botanique 56, 60. 1881.

[3] Oekologische Pflanzengeographie 304. 1896.

[4] Indomalayische Strandflora 68, 73. 1891.

[5] Bull. Soc. Roy. Bot. Belg. 32[1] :—. 1893. (Mém. p. 8).

While at Woods Hole, on the coast of Massachusetts, last July, it occurred to the writer to make a number of tests for soluble salts in the sands of the dunes and the beach, as well as in soils that are under water at high tide and bear a typical salt marsh vegetation. In September of the same year an opportunity offered to examine the sands of Long Beach, near Los Angeles, California. As a considerable difference was noted between the results obtained at Woods Hole and at Long Beach, a trip was made early in December to the neighborhood of Norfolk, Virginia, where soils of the dunes, the beach, and the salt marsh were examined.

In all cases the salt content of the soil was determined by the method employed in the Bureau of Soils of the U. S. Department of Agriculture and extensively applied by the bureau in its investigations of saline soils in the arid parts of the United States.[6] By means of an auger having a screw-diameter of 4^{cm} and a shaft of any length desired, marked at intervals of 3^{dm}, borings are made into the soil, which is brought up on the thread of the screw. Each 3^{dm} of soil is separately examined. After being thoroughly mixed, distilled water is added to the soil in quantity sufficient to saturate it. A cell of determined capacity is then filled with the saturated soil and the electrical resistance is taken by means of the Wheatstone electrolytic bridge. Correction is then made for temperature, 15.5° C. being taken as the standard. A further correction for soil texture is made. By a simple calculation the percentage by weight of water-soluble salts to soil can then be determined from the electrical resistance in ohms of the soil solution. Hundreds of determinations have been made by the Bureau of Soils in which both the electrolytic method and the method of chemical analysis have been applied to the same sample of soil, in order to determine its content of salts readily soluble in water; and these have demonstrated that the former method is sufficiently accurate for all purposes of the present inquiry.[7]

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[6] A full description of this method is given in "Instruction to field parties," Bureau of Soils (1903). The apparatus used is described in Bull. 15, Division of Soils.

First of all let us consider the salt marsh soils, which are inundated at every high tide. Two borings in such soil were made on the Massachusetts coast, the first to a depth of 6^{dm} in coarse gravelly sand, standing water being reached at $4-5^{dm}$. The boring was made amid a luxuriant growth of *Salicornia herbacea*, with some *Statice Limonium caroliniana;* while *Distichlis spicata* and *Suaeda maritima* occurred near by. Here the first 3^{dm} contained 1.5, and the second 1.4 per cent. of salt. The second boring was taken about 8^{dm} farther from the shore. Here standing water appeared at a depth of $2-3^{dm}$, precluding carrying the boring any deeper, and the coarse sand was mixed with some silt and considerable vegetable matter. The vegetation consisted of *Spartina stricta glabra* and a species of Fucus, with *Salicornia herbacea*, the latter smaller and less abundant than where the first sample was taken. Salt was present to the extent of 2.6 per cent. Near Norfolk, Virginia, a 6^{dm} boring was made in a narrow strip of marsh bordering a tidal inlet amid a fine growth of *Spartina stricta glabra.* The soil was a yellow sandy loam to a depth of about 4^{dm}, below that a blue clay, standing water being reached in the second 3^{dm}. Only 0.32 per cent. of salt was found here in the first 3^{dm}, and 0.29 per cent. in the second, although this spot is under water every day at high tide.[8] The lateness of the season (December 2), and consequently reduced evaporation from the soil when exposed at ebb tide, may partly account for the unexpectedly small amount of salt found. Otherwise we must admit a very wide range of salt content in the soil of salt marshes on the same coast, only a few hundred miles apart, since on the Massachusetts coast, all other conditions being quite similar, more than eight times as much salt occurred in the surface 3^{dm}.

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[7] A sample of salt marsh soil collected in the course of this investigation showed by the electrolytic method the presence of 0.30 and by chemical analysis 0.27 per cent. of soluble salts.

The results obtained on the Massachusetts coast are sufficient, nevertheless, to indicate that the soil of salt marshes is highly saline, at least during certain seasons of the year, and that the ecological peculiarities of their vegetation may safely be attributed, in large part, to this factor. Yet, we may observe in passing, there are large tracts of land remote from the coast, in the arid parts of North America, which contain still greater amounts of soluble salts and bear a vegetation of even more pronouncedly halophytic character than the marshes of the Atlantic coast.[9]

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[8] A chemical analysis of this soil was obtained through the courtesy of Dr. F. K. Cameron of the Bureau of Soils, U. S. Department of Agriculture. The total content of salts readily soluble in water in the sample analyzed was 0.27 per cent. (of total weight of soil), made up as follows:

1. BASES AND ACIDS.	
Calcium	trace
Magnesium	2.19
Sodium	27.73
Potassium	8.03
Sulfions	16.79
Chlorid	40.88
Carbonic acid	4.38
	100.00

2. CONVENTIONAL COMBINATIONS.	
Magnesium sulfate	10.22
Potassium chlorid	15.33
Sodium chlorid	55.48
Sodium sulfate	13.14
Sodium bicarbonate	5.83
	100.00

[9] Thus a number of examinations of saline soils in southern Arizona showed that *Suaeda Torreyana* will grow in the presence of 3.5 per cent. of salt in the surface 3^{dm} of the soil, and of an average for the upper 9^{dm} of 3 per cent.; *Sarcobatus vermicularis*, where an equal amount occurs; *Allenrolfea* (*Spirostachys*) *occidentalis* in the presence of 3.1 per cent. in the surface 3^{dm}, an average of 2.7 per cent. in the first 9^{dm}, and an average of 0.75 per cent. in the first 18^{dm}; *Atriplex lentiformis* where 3.3 per cent. of salt in the surface 3^{dm}, and an average of 1.6 per cent. in the first 9^{dm} occurs. In the San Joaquin Valley, in central California, "salt grass" (*Distichlis spicata*), a rather shallow-rooting plant, grows vigorously in the presence of 3.3 per cent. of soluble salts in the surface 3^{dm} of the soil.

Turning now to the beach and dune sands the results are tabulated for convenient reference as follows:

Locality	Situation where sample was taken	Salt content (in percentages of soil) at various depths		
		0–3 dm	4–6 dm	7–9 dm
Woods Hole, Mass.	Dune marsh	0.003	.....	.....
" "	Inner dune	0.003	.....	.....
" "	Beach, outer limit vegetation	0.006	0.004	.....
" "	Beach near outer limit vegetation	0.003	.....	.....
Norfolk, Va.	Low dune, inside outermost	0.004	0.004	0.007
" "	Break in outermost line dunes	0.03	0.02	0.02
" "	Beach, outer limit vegetation	0.003	0.009	0.006
" "	Beach, outer limit vegetation	0.004	0.003	0.003
Long Beach, Calif.	Beach, near outer limit veg.	0.14	0.02	.....
" "	" "	0.12	0.12	.....
" "	" "	0.13	0.13	.....
" "	" "	0.13	0.06	.....
" "	" "	0.15	0.12	.....

It is evident that we have here a condition as regards salt content of the soil quite different from that prevailing in the salt marshes. In order to a proper interpretation of these results some details of the examinations which yielded them must be given. On the Massachusetts coast a small "dune marsh," a level expanse among the dunes, covered with a thick carpet of vegetation—*Utricularia cornuta*, *Oxycoccus macrocarpus*, *Drosera intermedia*, *Lycopodium inundatum*—was first examined. Here a 3^{dm} boring into the coarse moist sand, of which the uppermost 3–6^{dm} contained a little vegetable matter, revealed the presence of only about 0.003 per cent. of salt. But in view of the character of the vegetation no considerable amount of salt was expected here.

An examination of the dunes themselves was the next step in the investigation. A low dune, some distance inside the outermost line of dunes, was selected for examination. Here the soil was a nearly pure coarse quartz sand, practically devoid of humus, and was quite moist immediately beneath the surface, as was found to be generally the case with the dune sands, as well as with those of the outer beach. This dune was covered with a growth of *Ammophila arenaria* and *Hudsonia tomentosa*. The first

3^{dm} of soil taken here had an electrical resistance too high to be read with the instrument used, indicating an amount of soluble salt too small to warrant carrying the boring deeper.

On the Virginia coast, a 9^{dm} boring was made into a low dune, just inside the outermost line of dunes (that which forms the landward limit of the beach proper). Here again the soil was a nearly pure quartz sand containing merely a trace of vegetable matter. While moist very nearly to the surface, the sand at a depth of $6–9^{dm}$ had a considerably greater water content and was also decidedly coarser than that nearer the surface. The vegetation consisted solely of a showy grass, the "sea oats" (*Uniola paniculata*).[10] Here the first 3^{dm} of soil contained about 0.004 per cent. of water-soluble salts, the second also about 0.004 per cent., and the third about 0.007 per cent.

Another 9^{dm} boring was made where a break occurred in the line of low outermost dunes, not far above the reach of the highest tides (as was shown by the presence of much driftwood just beyond), but at least 6^{m} back from the actual limit of high tide at the time the boring was made. It was about 2^{m} nearer the beach than the boring just described. Here the vegetation consisted of Ammophila and *Panicum amarum minus*. The soil was a rather fine, nearly pure quartz sand, moderately moist in the first 3^{dm}, quite moist below that depth. The salt content of the first 3^{dm} was about 0.03 per cent., of the second about 0.02 per cent., and of the third also about 0.02 per cent. Hence, for the 9^{dm} column of soil the proportion of soluble salts to total weight of soil was here about five times as great as in the dune covered with Uniola. This large difference is not easy to explain, although a somewhat smaller salt content in the dune would naturally be expected, as it was higher above sea level and farther from the high tide line.

It was of course anticipated that borings made on the beach proper, outside the outermost line of dunes, would reveal a greater salt content in the sand than was found in the boring just described, but such did not prove to be the case. On the Virginia coast two borings, each to a depth of 9^{dm}, were made along the line marking the outermost limit of vegetation towards the waves, one only a few meters distant from the boring in the breach in the outermost line of dunes just described, the other within a quarter of a mile of the first. In both cases the soil was a rather coarse quartz sand, with traces of decaying vegetable matter, quite moist to within $2–3^{cm}$ of the surface. The first boring was about 1.5^{m} outside the outermost line of dunes, and $4–5^{m}$ above the limit reached by flood tide at the date of the examination. Small plants of *Panicum amarum minus* grew where the boring was made. Here the resistance given by the saturated soil indicated in the first 3^{dm} about 0.003 per cent. of water-soluble salts, in the second about 0.009 per cent., and in the third about 0.006 per cent. Hence the percentage of salt in the 9^{dm} of sand was only about one-fourth as great as in the opening in the line of outermost dunes. It corresponds very closely, inexplicable though the fact may appear, with that of the dune covered with Uniola, which was still farther from the waves than was the opening through the dunes. The second boring on the outer beach was made amid small plants of *Ammophila arenaria* and *Salsola Kali*, about 5^{m} outside the outermost line of dunes and a considerable distance above the limit reached at that season by flood tide. Here the electrical resistance of the saturated soil indicated about 0.004 per cent. of salts in the first 3^{dm}, about 0.003 per cent. in the second, and about 0.003 per cent. in the third.

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[10] An account of this grass, as well as of other plants mentioned here, is given by the writer in his papers on "The plant covering of Ocracoke Island," Contrib. U. S. Nat. Herb. **5**: 261–319. 1900, and on "A botanical survey of the Dismal Swamp region," *ibid.* 321–550. 1901. A general ecological-geographical description of the vegetation of the North Carolina and Virginia strand is presented in the papers cited.

In the sands of the outer beach on the coast of Massachusetts two borings were made in July. The first sample for examination was taken at the outer limit of vegetation, which in this case extended only abont 1^{m} beyond the seaward base of the low outermost dunes. A luxuriant growth of *Ammodenia* (*Arenaria*) *peploides* occurred there, with *Atriplex arenaria* and *Ammophila arenaria* near by. The soil was a nearly pure quartz sand, moist as usual just below the surface. The boring was made to a depth of 6^{dm}, the first 3^{dm} giving an electrical resistance indicating about 0.006 per cent. of water-soluble salts, the second about 0.004 per cent. The results here were therefore closely comparable with those of the two borings made in December on the outer beach in Virginia.[11]

The second boring on the Massachusetts beach was made to a depth of only 3^{dm}, on the outer limit of vegetation, at a point where a small tidal inlet crosses the beach. The coarse sand here contained considerable partially decayed vegetable matter (chiefly Zostera) and was nearly saturated with water. The vegetation consisted of numerous vigorous plants of *Cakile americana*, and a few plants each of *Salsola Kali*, *Ammodenia peploides*, *Atriplex arenaria*, *Ammophila arenaria*, and *Xanthium* sp. The electrical resistance of the water-saturated sand here indicated the presence of about 0.03 per cent. of salts—about six times as much as was found in the first 3^{dm} of the preceding boring. This difference was doubtless due to the second boring having been taken at a point nearer the level of flood tide and quite close to the bank of a tidal inlet.

All the beach and dune soils examined along the Atlantic coast of the United States contained a considerable amount of water at a slight depth below the surface, which is indeed a well-known peculiarity of such soils. The data just given make it sufficiently evident that this water does not come from the sea, unless we can assume that sea-water, moving through but a few meters of sand, will give up nearly all the soluble salts it normally contains.[12] This assumption is *a priori* unlikely, and we are justified in concluding that this water comes from the other direction, and represents an underground movement, toward the sea, of water that had fallen as rain upon the soil farther inland. If this be the case, we need not be surprised that the salt content of sea beach soils appears to be generally very small, notwithstanding that considerable amounts of sea salt are probably at times deposited upon the beach by unusually high tides, and by spray from the waves. For in addition to this lateral movement of fresh water that drains from inland soils into the sea, the rain water that falls directly upon the beach and the dunes must cause a rapid leaching of soluble salts out of these coarse-textured soils, quickly carrying the salts to the depth at which the lateral flow of the soil water towards the sea is encountered.

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[11] The remarkably small amounts of salts present in the dune and beach soils just described would indicate a deficiency of mineral plant food, in view of the fact that cultivated soils in the eastern United States usually contain at least 0.02 per cent. of matter soluble in water. Perhaps to such deficiency may partly be ascribed the habit of many strand plants, particularly grasses, of extending their stems or roots so extensively over or through the soil. The necessity for feeding over the largest possible area of the sterile soil may cooperate with the necessity for the firmest possible foothold in the shifting, unstable sand in producing this habit of growth.

[12] A great number of samples of ocean water were taken on the Challenger Expedition. Of these a sample of surface water from near the latitude of Woods Hole (lat. 40°17′ N., long. 66°48′ W.) contained 3.287 parts per 100 of total solids, as estimated by Dittmar's method from the chlorin content; while a sample of bottom

An examination of the salt content of beach sands on the Pacific coast of the United States affords data for an interesting comparision with conditions on the Atlantic coast, as just described. Five borings, each to a depth of 6^{dm}, and all within a few meters of one another, were made at Long Beach, near Los Angeles, California. Here, as is the case with a great part of the coast of California, the beach is but a narrow strip of sand, limited on the landward side by a line of perpendicular

water from lat. 35° 58′ N., long. 70° 35′ W. (hence somewhat north of the latitude of Cape Hatteras) contained 3.611 parts per 100 (Rep. Challenger Exp. 1:41, 43. 1884). Dr. Joseph S. Chamberlain determined the mean total solids in three samples of sea water taken at Woods Hole in July 1902 to be 3.206 parts per 100, using Dittmar's method of calculating from the chlorin content. A sample taken at Woods Hole in April of the same year, analyzed by Dr. A. P. Saunders, gave 3.192 parts per 100. Dittmar (*ibid.*, p. 203) found the composition of the solids in sea water, in various parts of the world and at different depths, to be remarkably uniform. Taking the average of 77 samples, his results in parts per 100 of total solids are as follows:

Chlorin	55.292
Bromin	0.188
Sulfuric acid (SO_3)	6.410
Carbonic acid (CO_2)	0.152
Lime (CaO)	1.676
Magnesia (MgO)	6.209
Potash (K_2O)	1.332
Soda (Na_2O)	41.234
Basic oxygen equivalent to the halogens	−12.493
	100.000

cliffs. Well-developed dunes are wanting. The soil is a nearly pure quartz sand, much finer than that examined on the coast of Massachusetts and of Virginia, and contained much less water at the time the examination was made than is usually the case on the Atlantic coast. The vegetation amid which the borings were made comprised *Abronia maritima*—with round fleshy leaves and showy crimson flowers, *Franseria bipinnatifida*, *Distichlis spicata*, the succulent glaucous *Heliotropium Curassavicum*, *Suaeda* sp. (perhaps *S. Torreyana*), and *Atriplex leucophylla.* It is noteworthy that in three of these plants—Abronia, Heliotropium, and Suaeda—succulency is very highly developed. Heliotropium, Suaeda, and Distichlis are also characteristic plants of the highly saline soils of the interior of California.

These borings at Long Beach showed a quite uniform salt content for the first 3^{dm} of soil, ranging only from 0.12 to 0.15 per cent. of water-soluble salts. At a depth of $4–6^{dm}$ the differences between the several borings were more pronounced, the maximum content being 0.13 per cent. and the minimum 0.02. The mean salt content, as indicated by the five borings, is about 0.13 per cent. in the first 3^{dm}, and 0.09 per cent. in the second.[13]

[13] A chemical analysis of this soil was obligingly furnished by Dr. Cameron. The total salt content for the upper 6^{dm} of soil was found to be 0.22 per cent. in the sample examined. The composition is as follows, each component being stated in percentages of the total amount of water-soluble salts in the soil:

1. ACIDS AND BASES	
Calcium	2.72
Magnesium	3.63
Sodium	20.91
Potassium	7.27
Sulfions (SO_4)	20.00
Chlorin	31.84
Carbonic acid (HCO_3)	13.63
	100.00

2. CONVENTIONAL COMBINATIONS	
Calcium sulfate	9.09
Magnesium sulfate	17.28
Potassium chlorid	13.63
Sodium chlorid	41.82
Sodium bicarbonate	18.18
	100.00

Comparing this analysis with that of a salt marsh soil on p. 427, we note that magnesium, sodium, and potassium correspond pretty closely in both soils. As would be expected, the easily leached-out chlorids are relatively more abundant in the marsh than in the beach soil, while the converse holds true of sulfates, a considerable portion of which is doubtless the relatively insoluble calcium sulfate. It is interesting that while the marsh soil contains a mere trace of calcium (not determinable quantitatively by ordinary methods), the beach sand contains a considerable amount of this base. This difference may be accounted for by the fact that in the sea water, which is occasionally deposited on the beach by winds and very high tides, calcium carbonate is one of the first substances precipitated as the water evaporates, and is one of the

We have then a much higher content of soluble salts in the beach sands of the coast of southern California than in corresponding situations on the Atlantic coast of the United States. The fact that the sand was much drier at Long Beach than in the localities examined in Massachusetts and Virginia gives us the clue for a probable explanation of this difference. In all likelihood, climatic differences between the two regions, especially as regards quantity and distribution of the rainfall, account for this marked difference in the salt content of the soils. Where the rainfall is slight, either throughout the year or at some one season, the concentration of the soil solution must correspondingly increase, for evaporation from the surface is constantly going forward. The same climatic conditions which cause the formation of extensive tracts of saline soil in the interior of continents will, *caeteris paribus*, bring about a similar result along the coast. The mean annual rainfall at Los Angeles is 39.3^{cm}, and normally only 0.5^{cm} falls in that region between June 1 and September 30. At the time the results just described were obtained (September 29, 1903), only 1.12^{cm} of rain had fallen during the previous four months.

At Norfolk, on the other hand, the mean annual rainfall is 130.2^{cm}, and during the four months from June 1 to September 30, it is 52.05^{cm}. In the two months preceding the date on which the soil samples above described were taken, *i. e.*, October and November 1903, 20.5^{cm} of rain fell. Furthermore, in the season of the year when the examination was made near Norfolk (December 2), evaporation must be considerably reduced and the tendency towards a concentration of salts near the surface of the soil due to this cause, in conjunction with the capillary rise of water in the soil, must be considerably less than during the summer. However, the results obtained in midsummer on the coast of Massachusetts, where conditions as to rainfall are much like those on the Virginia coast, go to show that the concentra-

last components to be leached out of the soil by subsequent rainfall. In salt marsh soils, on the other hand, the daily ebb and flow of the tide prevents any marked accumulation by evaporation of such calcium salts as are deposited. But the possibility that part, at least, of this calcium is carried into the beach sands from soils farther inland cannot be ignored, since California soils are often very rich in lime.

tion of the soil solution in beach sands of the Atlantic coast of the United States must be at all times considerably less than on the California coast. This is further confirmed by the character of the vegetation, which is more decidedly halophytic on the California than on the Atlantic coast.

This brings us to the question which serves as the title for this paper. In the light of the investigations just described, are we justified in classifying the vegetation of sea beaches and dunes as halophytic?[14]

If the soil is not saline, or but slightly so, while the climatic conditions are such as to render protection against excessive transpiration necessary, it is obvious that the vegetation, while xerophytic, is not halophytic.

Ordinary cultivated soils of the eastern United States generally contain matter readily soluble in water to the amount of 0.02 to 0.2 per cent. (by weight to dry weight of soil).[15] Now the greatest concentration of soil solution found in beach sands in the course of these investigations—at Long Beach, on the coast of California—does not exceed the maximum occurring in ordinary cultivated soils, according to the above figures. On the Atlantic strand the salt content of the sand is generally far below the minimum present in ordinary cultivated soils, if not actually too small to supply the optimum amount of mineral nutrients required by most cultivated plants.

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[14] In employing this term we do not lose sight of the fact that halophytes do not constitute an ecological class coordinate with hydrophytes and xerophytes, but are properly only a subdivision of the latter. Like other xerophytes, they are characterized chiefly by the possession of various adaptations for reducing transpiration, as Warming (Halofyt-Studie, p. 235) and Schimper (Pflanzengeographie, p. 99) have pointed out. Halophytes are such xerophytes as owe their necessity for a reduction of transpiration largely to the presence in the soil of an excessive amount of readily soluble salts. The character of the soil is the final criterion which decides whether we shall call a given vegetation halophytic or non-halophytic. No ecological characters can be cited as exclusively halophytic, although halophytes seem to show a more marked tendency than other xerophytes toward a development of water-storage parenchyma. In halophytes the xerophytic habit is often developed to an extreme. This is what we should *a priori* expect, since saline soils are generally found in places where the climatic conditions (apart from peculiarities of the soil) tend to a development of xerophytic characters, as along the sea coast and in desert regions. The addition of a soil factor that makes absorption of water by the roots difficult (as is perhaps the case when salts are present in excessive amount) to climatic factors which tend to cause excessive transpiration from the leaves and stems should necessitate development in the plant of every possible means for hoarding its water content.

[15] Data as to the amounts of salts in the soil solution endurable by various cultivated plants not regarded as peculiarly resistant, are afforded by the very numerous examinations of cultivated soils that have been made by the Bureau of Soils in the arid western part of the United States. The bureau has found that lucerne, when young, will endure 0.4 per cent., in later stages of development 0.6 to 1.0 per cent. of water-soluble salts; wheat, something less than 0.4 per cent.; barley, seedlings 0.6 per cent., older plants 1.0 per cent. The writer has found in Egypt the cotton plant maturing its fiber in the presence of 1.0 per cent. of salts in the surface 3^{dm} of the soil; and in Arizona in the presence of 0.9 per cent. in the first meter of soil.

So far as the data yet available may warrant a generalization, we must therefore conclude that plants of sandy sea beaches and dunes are not generally halophytic, although, as is the case at Long Beach, species that are elsewhere characteristic of strongly saline soils and belong to truly halophytic associations may enter into the vegetation of the sand strand.

We must look to factors of the physical environment other than an excessive concentration of the soil solution for an explanation of the usually distinctly xerophytic character of sand-strand vegetation. Among such factors may be mentioned strong winds (often carrying salt spray from the surf), intense light and a great amount of heat radiated from the surface of the sand in summer, all of which would doubtless have a share in bringing about excessive transpiration from plant surfaces not protected by special adaptations. To these factors then we must attribute the occurrence in plants of the sand strand (although growing in a soil usually amply supplied with water and in an atmosphere often nearly saturated with moisture) of many of those modifications of structure by which desert plants protect themselves against excessive loss of water by transpiration. All these conditions of the environment are common as well to the sandy beaches of great freshwater lakes, so that it is in no way remarkable, from an ecological point of view, that such typical sea coast plants, for example, as *Ammophila arenaria*, *Cakile americana*, *Lathyrus maritimus*, and *Euphorbia polygonifolia* are likewise found on the shores of Lake Michigan.

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